THE SUCCESSIONAL STATUS OF *CUPRESSUS ARIZONICA*

Albert J. Parker

ABSTRACT.— Several investigations (size-class analysis, age-determination inquiries, and germination tests) suggest that *Cupressus arizonica* of southeastern Arizona is a pioneer species. The tree requires disturbance to remove or reduce soil litter, which otherwise inhibits the reproduction of the species. Reduction of light intensity caused by canopy closure appears to be less important than litter accumulation in restricting *C. arizonica* reproduction. Following disturbance, successful establishment of seedlings may occur over an extended period (50 to 100 years), as litter gradually accumulates. The absence of *C. arizonica* seedlings in present populations suggest that fire suppression policies on federal lands where *C. arizonica* occurs have altered fire frequency, and consequently have fostered a short-term reduction in *C. arizonica* establishment. Only in floodplain environments, where flooding disturbs the soil surface, has much reproduction occurred in recent years. The long-term population pattern of *C. arizonica* appears stable, due to the great longevity of the species.

Rough-barked Arizona cypress (*Cupressus arizonica* Greene; all taxonomy after Kearney and Peebles 1960) is a tree species of local occurrence in the mountain ranges of southeastern Arizona, southwestern New Mexico, western Texas, and northern Mexico. Though it has typically been characterized as a moisture demanding species of riparian association (Wolf 1948a, Whittaker and Niering 1965, Brown and Lowe 1974), recent findings (Parker 1980) demonstrate that *C. arizonica* may occupy relatively xeric landscape positions—including south-facing slopes, ridge tops, and convex slope configurations—at higher elevations (around 2000 m).

In the first published report mentioning *Cupressus arizonica* regeneration, Posey and Goggans (1967) observed little reproduction anywhere in the Southwest, although they collected no data to substantiate or investigate this phenomena. They did express concern that the limited natural range of the species, coupled with its apparent inability to reproduce in many natural circumstances, could indicate that its existence was threatened. This paper investigates the population dynamics, reproductive strategy, and role in species replacement processes of *C. arizonica* in the upland forests of southeastern Arizona.
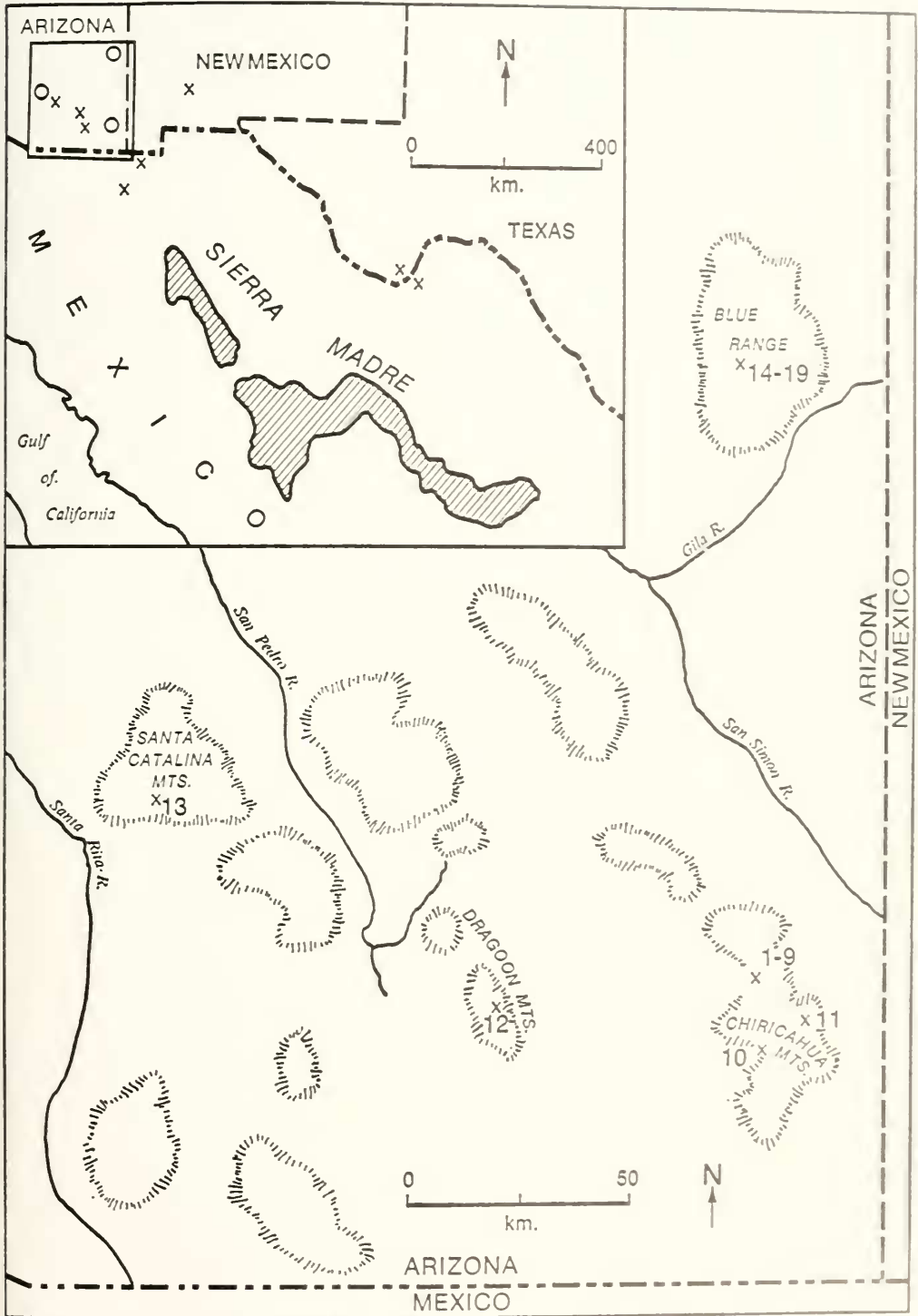
STUDY AREAS

Populations of *Cupressus arizonica* were sampled in the Chiricahua Mountains, the Blue Range north of Clifton, the Dragoon Mountains, and the Santa Catalina Mountains, all located in Arizona (Fig. 1). *Cupressus arizonica* is most common in the woodland zone of these mountain ranges (1300–1900 m; Whittaker and Niering 1965), a zone characterized by the frequent co-dominance of alligator juniper (*Juniperus deppeana*), pinyons (*Pinus cembroides* and *P. edulis*), and a number of oak species, including silverleaf oak (*Quercus hypoleucoides*), netleaf oak (*Q. rugosa*), and Arizona white oak (*Q. arizonica*). *Cupressus arizonica* is progressively more restricted to riparian habitats where the woodland zone grades into the shrub-dominated desert and semidesert vegetation types below. It is also found in stands at higher elevations (1600–2300 m) with other conifers, notably Arizona pine (*Pinus ponderosa* var. *arizonica*), Apache pine (*P. engelmannii*), Chihuahua pine (*P. leiophylla*), and Douglas-fir (*Pseudotsuga menziesii*); these forested stands often have closed canopies.

The climate of the woodland zone is subhumid and mild, with about 50 cm annual precipitation and a mean annual temperature of 12.5 C. The wettest periods of the year are middle to late summer and midwinter (Bryson and Lowry 1955).

The isolated mountain ranges of this region of basin and range topography are roughly linearly aligned, northward trending, and

Department of Geography, University of Georgia, Athens, Georgia 30602.

Fig. 1. Study area with the species range inset. The location of stands included in this study are noted by number. Open circles in the inset represent the three extensive areas of nonriparian *C. arizonica* occurrence in southeastern Arizona: the Chiricahua Mountains, the Blue Range, and the Santa Catalina Mountains.

separated by extensive sediment-filled lowlands. The bedrock core of these ranges include both igneous and sedimentary rocks (Fenneman 1931).

METHODS

Environmental and vegetational measurements were obtained from 19 internally homogeneous stands of *C. arizonica*. Within each stand, three 4 by 25 m quadrats were oriented so that their central long axes were normal to a contour line bisecting the stand, with intervals of 10 m separating each quadrat. The following measurements were recorded within each quadrat: the species and circumference at breast height (1.37 m) of each tree, the number of saplings of all tree species, and the number of *C. arizonica* seedlings. Any stem of at least 20 cm circumference at breast height was considered a tree. A sapling was defined as the stem of any tree species which exceeded breast height, but which was less than 20 cm in circumference at that height. All stems of tree species less than breast height were counted as seedlings. The depth of the litter layer in each stand was measured at 1 m intervals along the central long axis of each quadrat. A total of 60 litter depth measurements was made per stand.

In two stands, both in the Chiricahua Mountains, all *C. arizonica* trees with a circumference at breast height exceeding 30 cm were cored with an increment borer at breast height. These two stands were chosen for their differing size structures. One stand was characterized by trees few in number but large in diameter, but the other stand had a great number of individuals, particularly in the smaller size-classes. These two stands were selected as representative of 14 of the 19 stands sampled. The other five stands has a size structure intermediate in character between those chosen for coring. In total, 79 trees were cored.

Cores were aged in the laboratory, although the aging was complicated by two factors. First, several of the *C. arizonica* trees possessed rotted xylem tissue that caused fragmentation of some cores and loss of record from the damaged segments. Second, *C. arizonica* has been shown to produce false an-

nual rings (Bannan 1954). To circumvent the first difficulty, the length of each core was measured and the following formula was used to compute a "tree ring" age for each sample:

$$0.95 \left(\frac{c}{2\pi}\right)(g) = t$$

where: t = extrapolated tree ring age (yr)
c = circumference of the tree (cm)

g = number of annual rings per unit length of core (yr·cm^{-1}; this value is later referred to as "mean time required per unit of radial growth")

0.95 = a coefficient to adjust for bark thickness

With respect to the second complication, Glock and Agerter (1963) were able to utilize microclimatic records from a plantation of *C. arizonica* near Lubbock, Texas (500 km from the species' natural range) to investigate the production of false annual rings in this species. They reported that multiple false rings may be produced by an individual in a single year, and that the number of false rings is not consistent from tree to tree, or even from place to place on the same tree. Because of these difficulties, precise absolute aging was not possible, and tree ring ages reported in this study may be as much as two times larger than the actual tree age. Nevertheless, the ring counts and extrapolated ages provide an indication of the relative ages of individuals and thus allow identification and interpretation of the approximate age structures of the stands.

Cones of *C. arizonica* were collected for the purpose of determining the mean number of seeds per cone, as well as to provide seeds for use in germination tests. All 250 cones collected were from the second year foliage of a number of *C. arizonica* individuals located in the Blue Range. Only closed cones were collected. Fifty of these cones were randomly selected, and seeds from each cone were counted. Following this, the other cones were emptied of seeds, and all seeds were then sorted by size, the larger seeds being kept for use in germination tests.

A series of germination tests were performed on lots of 100 seeds selected randomly from the seed source. These tests in-

vestigated the relationship of *C. arizonica* germination success to the following factors: freezing, flooding, fire, litter buildup, and light intensity. The physical conditions in which the germination tests were performed followed those of Wolf (1948b) in general (see Table 4).

RESULTS

Stands were segregated into three groups, according to the size-class frequency distribution of individuals of *Cupressus arizonica*. The eight stands of the first group display a

generally logarithmatic decrease in the number of individuals in successively larger size-classes, with the exception that the seedling layer is virtually absent (Fig. 2). Populations with a size structure similar to that of the first group are often characterized as stable through time, with losses of canopy individuals being balanced by replacements from the sapling layer (Daubenmire 1968). The six stands of the third group, in contrast, lack a logarithmatic trend. Instead, the number of individuals in successively larger size-classes is more constant (Fig. 2), suggesting that a past period of reproduction has ended. The
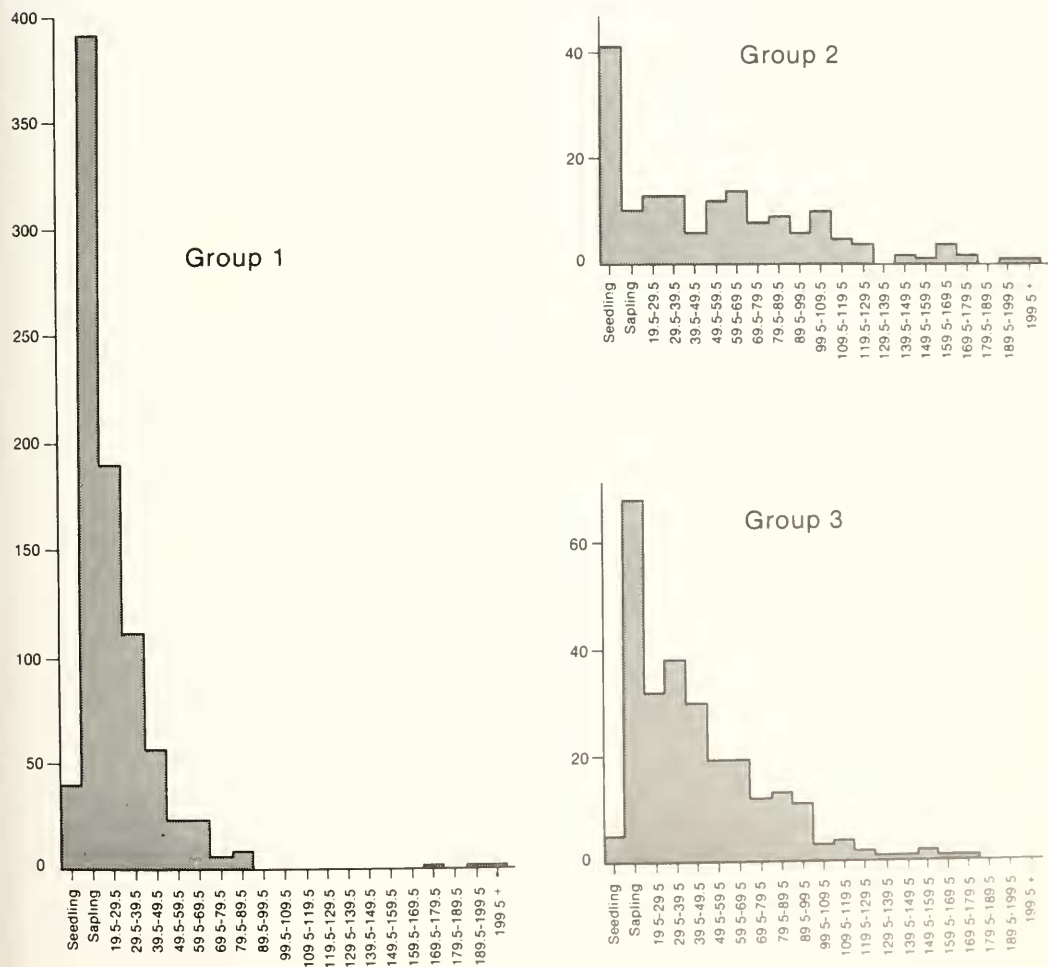

Fig. 2. Composite size-class structure histograms for stands of *C. arizonica*. See text for a definition of each of the three groups.

second group includes five stands intermediate in character between the other groups.

Even in those cases which appear to possess a steady-state population above the sapling layer, the almost universal absence of *C. arizonica* seedlings in stand understories (Table 1) is conspicuous, and agrees with the observation of Posey and Goggans (1967). Conditions in the two stands which do contain a relatively large number of seedlings are significant; in both cases, disturbance has exposed bare mineral soil, in one case by natural flooding and in the other by logging activities that mechanically stripped off the litter from a portion of the forest floor.

The behavior of other tree species in *C. arizonica*-dominated communities fall primarily into two types, according to stand size-class information (Table 2). A first group consists of intolerant pioneer species, which reproduce episodically in association with disturbance events, and probably depend on wide dispersal of seeds to maintain representation on a given site. These species display an even aged structure in most *C. arizonica* stands. The common upland conifers of the region, such as Apache pine, Arizona pine, and Douglas-fir fit this behavior pattern. A second group consists of tolerant species with stable populations that reproduce either vegetatively of by widespread dispersal from adjacent locales. These display continues reproduction in *C. arizonica*-dominated stands, with a maximum number of stems occurring in recent cohorts. This group includes the typical pinyon/oak woodland dominants—Mexican pinyon, silverleaf oak, netleaf oak, and Arizona white oak.

Core analysis indicated that the mean tree ring age of *C. arizonica* in the stand with few but large individuals was 317.1 years, with ages ranging from 197.6 to 456.7 years (Table 3). The majority of tree ring ages were between 250 and 375 years. No seedlings, saplings, or trees of less than 30 cm circumference at breast height were found in the stand. Thus, the tree ring age of the youngest *C. arizonica* individual was almost 200 years. The mean tree ring age of *C. arizonica* trees in the stand with the greater density of smaller trees was 116.9 years, with an age range from 62.4 to 178.1 years. However, there were also a large number of saplings and trees too small to core, and these size-classes probably extended the age range down to about 25 years. The conspicuous absence of *C. arizonica* seedlings in the understory of this stand (Table 3) suggested that reproduction has been inhibited during about the last quarter century.

To determine the degree to which understory individuals of *C. arizonica* were suppressed by the overstory, a linear correlation and regression analysis was performed on the mean time required for unit growth (yr·cm^{-1}) for each tree against tree radius. A negative correlation coefficient would be predicted in conditions of understory suppression, because small trees would require longer periods of time to produce an amount of radial growth equal to that produced on the larger, more rapidly growing trees in the canopy in a shorter period of time. The results suggest that suppression of understory individuals

TABLE 1.   The seedling class.

	No. seedlings	Mean
Recently flooded stand	20	—
Recently logged stand	36	—
All other stands (17)	17	1.0
Total	73	3.7

TABLE 2.   Composite size-class structures for upland conifers and pinyon-oak species. The figures heading each size-class category are the smallest possible circumference in that class, and size-classes include all stems up to the next larger value. Upland conifers include Arizona pine, ponderosa pine, Apache pine, and Douglas fir. Pinyons include Mexican pinyon and two-leafed pinyon. Oaks include silverleaf oak, netleaf oak, and Arizona white oak.

	Size-class (cm circumference)											
	sapl	20	30	40	50	60	70	80	90	100	110	120
Upland conifers	3	4	4	7	4	3	8	4	0	4	5	9
Pinyons	63	27	18	13	4	7	2	2	1	1	0	0
Oaks	111	27	18	24	18	8	4	3	0	1	0	1

TABLE 3.   Characteristics of cored stands.

	First stand	Second stand
Tree density (ha^{-1})	1333	3733
Total basal area (dm^2·ha^{-1})	11901	5854
Mean basal area of C. arizonica trees (dm^2·tree^{-1})	9.51	1.49
Number of C. arizonica cored	21	58
°Mean time required per unit growth of C. arizonica (yr·cm^{-1})	24.2	16.6
Mean extrapolated tree age of C. arizonica (yr)	317.1	116.9
Standard deviation of extrapolated tree age (yr)	63.0	26.4
Oldest C. arizonica extrapolated age (yr)	456.7	178.1
Youngest C. arizonica extrapolated age (yr)	197.6	62.4
Number of C. arizonica saplings and trees too small to core (20–30 cm)	0	81
Number of C. arizonica seedlings	0	0
Correlation coefficient for suppression test	–0.833	–0.673

°Calculated by dividing the number of annual rings per core by the length of that core, it expresses the number of years required for an individual to add one cm of radial growth and is the reciprocal of the growth rate.

The great number of seeds produced does not necessarily insure abundant reproduction. Sudworth (1915) noted that seeding of C. arizonica was best on moist, bare mineral soils. Field observations made during the course of data collection confirm this suggestion, in that C. arizonica reproduction was generally restricted to areas within 2 of the 19 stands, and then only on exposed mineral soil associated with recent floods or logging. Moreover, the weighted average of litter depth where C. arizonica seedlings were encountered (1.74 cm) was only half the mean depth of litter for all stands in this study (3.42 cm), indicating that successful reproduction is associated with reduced litter depth.

Germination tests also indicated that a litter layer sharply reduced the germination and survival of seedlings. Only 3.7 percent of the seeds germinated on the litter-covered substrate, in contrast to 10.0 percent on mineral soil controls (Table 4). Of the other factors tested, freezing of seeds prior to germination, reduced light intensity, and immersion of seeds in water did not alter germination success. Simulated exposure of seed-bearing cones to canopy fire conditions, while reducing germination success (6.0 per-

was evident in both stands (Table 3). The degree of suppression was greater in the older stand, as a consequence of the longer period of time over which competition was acting. These results indicate that small C. arizonica trees may persist beneath a canopy, and suggest that the species is shade tolerant.

Evidence from core aging also suggests that C. arizonica possesses potentially great longevity. Based on the rates of growth determined in this study (Table 3), and accounting for multiple annual rings, some of the larger individuals encountered in canyon bottoms (exceeding 1 m dbh) may be 300 to 500 years of age.

Not only does the species achieve old ages, but also it produces great numbers of seed. The mean number of seeds per cone was 104.2, with a standard deviation of 19.8. It was estimated that healthy trees of moderate size (50 cm circumference) may produce from 10^3 to 10^4 cones per year, therefore resulting in an annual seed crop per tree of from 10^5 to 10^6 seeds.

TABLE 4.   Germination test results. The soil in each pot was composed of a mixture of 50 percent sand and 50 percent silt loam. The surface was without litter cover. Pots were supplied with adequate water regularly and were grown under high levels of sunlight. The pots were 15 cm in diameter and allowed free drainage below. The air temperature was between 20 and 24 C throughout the duration of the tests.

Treatment	Number of test pots	Composite germination rates (%)
Litter cover over mineral substrate	6	3.7
Seeds exposed to freezing before planting	4	8.8
Seeds immersed in agitated water	2	10.0
°Seeds exposed to canopy fire conditions	1	6.0
°°Seeds exposed to ground fire conditions	1	0.0
Seeds grown under reduced light levels	2	8.5
°°°Controls	10	10.0

°–Cones filled with seeds were exposed to 80 C for eight minutes.
°°–Cones filled with seeds were exposed to 315 C for eight minutes.
°°°–Control conditions.

cent), did not destroy all seeds. In contrast, exposure to simulated ground fire conditions, which are much hotter, killed all seeds within the cones. Thus, *C. arizonica* seeds enclosed in cones on branches may remain viable after fires, and have the capability to germinate on the mineral seedbeds exposed by burning.

DISCUSSION

The absence of *C. arizonica* reproduction under adults of the same species in natural stands is striking. Two interpretations of this observed absence of young individuals are possible. First, successful reproduction may be temporally sporadic and linked to occasional optimal climatic conditions that foster waves of *C. arizonica* reproduction. If such optimal conditions have not occurred during the last 20 or 30 years, the paucity of *C. arizonica* seedlings would be explained. However, successful reproduction of *C. arizonica* was encountered in two recently disturbed habitats, and this indicates that recent climatic conditions are not inimical to the tree's reproduction. The environmental conditions associated with these cases of successful reproduction do support, however, a second interpretation of the absence of *C. arizonica* seedlings, namely, that disturbance is necessary to create conditions favorable for regeneration, and that factors associated with a closed forest inhibit seeding by the tree.

Stand size-class analyses would seem to both support and contradict this characterization of *C. arizonica* as a species requiring disturbance for reproduction. Stands of the first group suggest that the species is tolerant, able to maintain itself under a closed canopy through time. Stands of the second and third size-class groups imply that the species is intolerant, with a period of establishment, followed by the cessation of *C. arizonica* reproduction. Therefore, the latter groups support the hypothesis that the species is opportunistic, capable of invading open habitats, but not able to compete effectively with other species as successional processes proceed.

Inspection of core analyses resolve this apparent paradox. The first stand cored, representing those stands that are dominated by large individuals and which suggest that the species is a pioneer, possesses no individuals with a tree ring age of less than 200 years.

The trees from this stand exhibit a tendency to clump in the 250- to 375-year tree ring age range. Lack of successful *C. arizonica* regeneration over an extended period, combined with a tendency toward clumping of ages, suggests that, following a lengthy period of *C. arizonica* establishment, reproduction is virtually eliminated. The second stand cored, representing those stands with a mixed size structure and suggesting that the species is a climax-type, possesses trees ranging in tree ring age from 25 to 150 years. This stand possesses, however, a conspicuous absence of reproduction during the last quarter century. These data, in the same manner as those from the first stand, suggest that following a lengthy period of colonization and reproduction of *C. arizonica*, perhaps 50 to 100 years in length, reproduction subsequently ceases. The population structures of these two stands, therefore, differ only in the elapsed times since disturbance, rather than in some fundamental difference in the ecological behavior of the species. In both cases, *C. arizonica* acts as an intolerant species, requiring disturbance to create invadable habitats. In the denser, more youthful *C. arizonica* population of the second stand, disturbance was more recent than in the older population of *C. arizonica* in the first stand. The initial interpretation of stand structures of the first type—that the species is a climax-type, with a stable, self-perpetuating population—is shown to be incorrect. Stands of the first group attain this pseudoclimax type structure only temporarily as a consequence of the extended period following disturbance when *C. arizonica* reproduction is possible. Thus, the three groups identified by differing size structures may be interpreted as stages of a temporal continuum, with each stage reflecting a longer period of development since a disturbance event.

Other results yield evidence favoring the interpretation of *C. arizonica* as an intolerant species. The longevity of *C. arizonica* is characteristic of many pioneer species, as it increases the allowable length of time between periodic disturbances, thus enhancing the probability that perturbation will occur on or near the site while mature seed trees are available for colonization. Seed counts and estimated cone crop sizes indicate that *C.*

arizonica is a prolific seeder, also a characteristic of the reproductive strategy of a pioneer species, because it increases the probability that a germule will be dispersed to an open habitat. The inverse relationship of litter depth to *C. arizonica* seedling number indicates that partial or complete removal of litter on the forest floor is necessary to promote reproduction. The inhibition of litter on germination in test pots further corroborates the negative effects of litter accumulation on this tree's regeneration. This need for mineral seedbeds, created by natural disturbance (i.e., fire or flooding) or by certain human activities (i.e., logging) is typical of pioneer elements. Finally, the ability of seeds to remain viable following a canopy fire is an opportunistic character often favored by intolerant species that must colonize open habitats following such fires.

In contrast to the characteristics suggesting that *C. arizonica* is a pioneer species, the tree's abilities to germinate in low light conditions and to tolerate shaded sites by suppression of growth are characteristics more commonly associated with climax-type than with pioneer species. These responses to light are puzzling and deserve closer inspection in the future. In general, however, it is concluded that *C. arizonica* is a pioneer species, requiring periodic disturbance to open new sites for colonization.

A unique characteristic of *C. arizonica* stand dynamics is the long period, as long as a century, during which colonization and reproduction remain possible after the disturbance event. Jenny et al. (1949) have demonstrated that, in ponderosa pine forests at 1220 to 2220 m elevation in California, 100 to 200 years are required to reach a near-equilibrium steady-state condition of litter thickness, in which mineralization of organic matter balances the addition of litter produced by the vegetation. Such a long period of litter accumulation is characteristic of moist, cool montane conifer forest ecosystems, and fits well with the observed time scale of *C. arizonica* establishment on a site. This peculiarly long period of colonization appears to be related to the shade-tolerant character of the species. Most pioneer species, being intolerant, rapidly cease reproduction as light levels decrease under the species' own canopy. The ability of *C. arizonica* to reproduce in shade allows it to continue reproducing for a much longer period than most colonizing species. This period is later terminated by the more gradual process of litter accumulation.

Thus, *C. arizonica* may be considered to be a pioneer species that is intolerant of litter accumulation under a closed canopy, even though it is tolerant of low light levels following colonization of disturbed sites. Additionally, its habit of seed persistence in the cone is critical to its maintenance on most sites. It may not depend, then, on seed dispersed from distant sources to colonize a given disturbed area.

Using the Noble and Slatyer (1977) model of successional processes (from Cattelino et al. 1979), this study suggests three types of species that exhibit fundamentally different responses to disturbance events. First, the upland conifers are DI species, characterized by widespread dispersal capabilities (D) and intolerance to a closed canopy (I). These trees depend on colonizing disturbed sites with seed from an off-site source. Second, the pinyon oak group are DT/VT species, which persist on a disturbed site by colonization from an off-site source (D—pinyon) or by vegetative reproduction (V—oaks). These species maintain themselves by virtue of their tolerance of closed canopy conditions (T). *Cupressus arizonica*, the third type, is a CI (DI) species. As described above, it is intolerant (I) of closed forest conditions and generally is maintained locally by seed persistence in cones from the canopy (C), which shelter viable seeds through disturbance events. Because of its limited range, *C. arizonica* is less commonly maintained by dispersal from adjacent populations (D), except perhaps in riparian stands, where surface water wash may supply seeds to wash environments from surrounding upland slopes.

These three types of species, in combination with differential longevity patterns, yield three possible pathways of community development (Fig. 3). The initial composition of each case is represented by at least one stand sampled in this study. The first and second cases diagram multiple successional pathways in communities which possess representatives of the three behavioral types. In the first case, the model assumes a greater
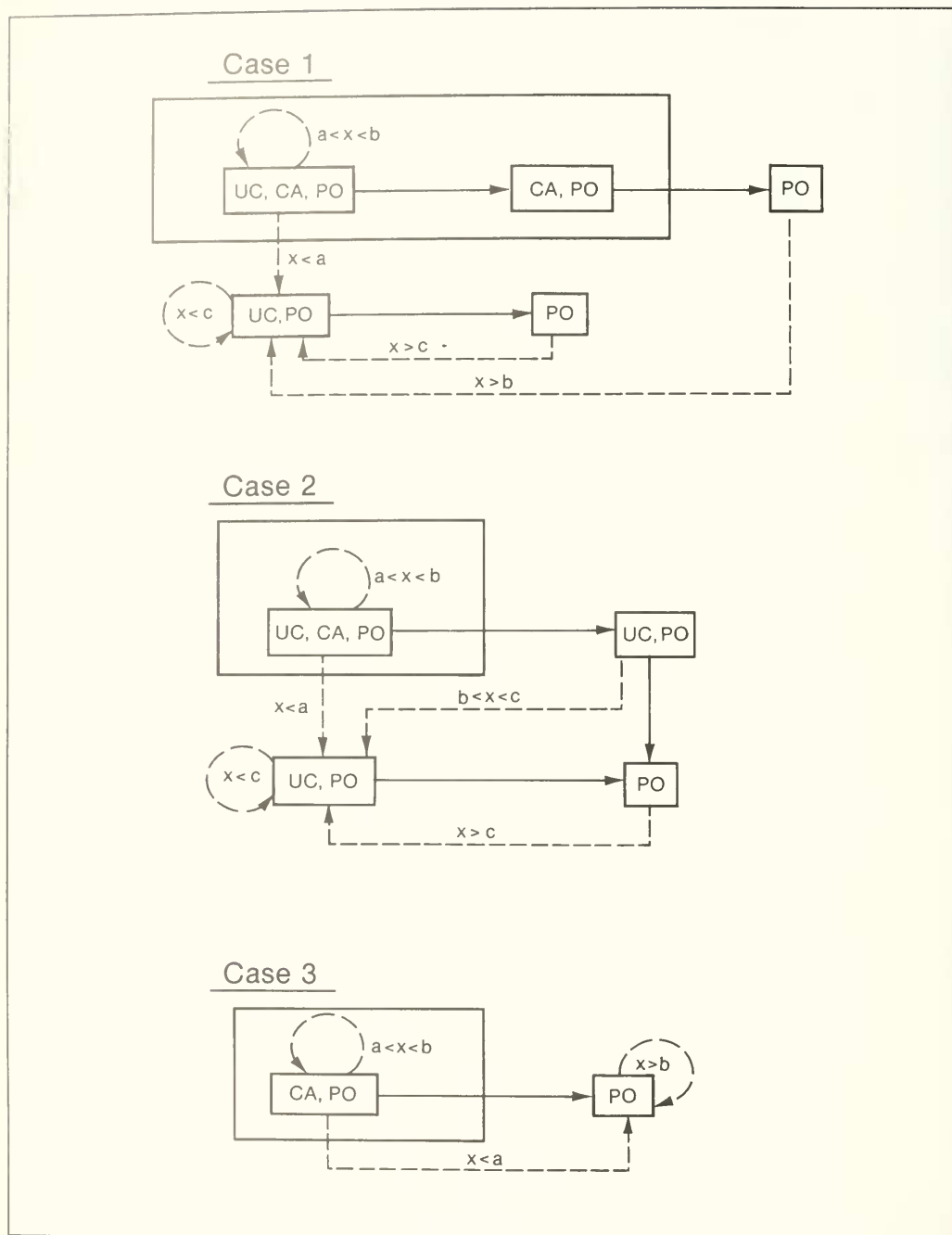
Fig. 3. Potential multiple pathways in a successional development model. Solid lines indicate developmental changes in the absence of disturbance. Dashed lines represent disturbance events. Boxes define the constraints on *C. arizonica* populations, if they are to avoid local extinction. Symbols:

UC   Upland conifers
CA   *Cupressus arizonica*
PO   Pinyon-oak species
  x   period of time since last catastrophic disturbance event
  a   time required by *C. arizonica* to reach maturity and produce seeds
  b   longevity of *C. arizonica*
  c   longevity of upland conifers

life span for *C. arizonica* than for the upland conifers, but in the second case the model assumes that upland conifers live longer than *C. arizonica*. In both cases, upland conifers are maintained indefinitely in the landscape by their wide dispersal of seeds, and pinyons and oaks are maintained by their tolerance to a closed forest canopy. *Cupressus arizonica*, however, may become locally extinct, depending on the timing of disturbance events. If disturbance recurs more frequently than the time required for *C. arizonica* maturity, the species will not be maintained in the community because the canopy seed reserve is destroyed. Such local extinction assumes that no introductions occur by dispersal from non-local populations, and that the disturbance was large enough in areal extent to kill the entire local population of *C. arizonica*. A second mechanism for local extinction in each case would be for disturbance to be so infrequent that the local population dies out before reinitiation of a successional cycle. The third case in the model represents a simplified community in which the upland conifer element is locally absent, whether by habitat restriction or chance.

It is apparent from this model of succession that, assuming habitat factors remain unchanged, local extinction of *C. arizonica* would occur only with excessively frequent or infrequent catastrophic fire events. Low net productivity and fuel loadings do not make frequent catastrophic fire a highly probable event in montane forests of southeastern Arizona. Suppression of fires by humans may temporarily reduce *C. arizonica* reproduction, but, unless the program is maintained effectively for several hundred years, it is unlikely to result in extinction of local populations.

The situation in riparian settings is even more favorable for *C. arizonica* perpetuation. In these habitats, population maintenance is effected by dispersal from adjacent upland populations, as well as by local preservation of seeds in the canopy. Extinction on such sites would require elimination, not only of the local population, but also of other *C. arizonica* populations higher in the watershed. Additionally, flooding assumes an important role as a disturbance mechanism in these stands. This is particularly significant

with respect to *C. arizonica* regeneration, because, while it may not increase surface light intensities, it will remove litter and expose bare mineral soil, which triggers reproduction, apparently irrespective of light conditions at the forest floor. (Certainly, light intensities influence growth rates and vigor, but not necessarily establishment potential.)

In effect, *C. arizonica* appears to be a stable, terminal element of the restricted habitats in which it presently occurs. Its life history characteristics (including its great potential longevity), population maintenance mechanisms, and colonization patterns combine to make it a persistent species, threatened in a temporal sense only by the remote probability of either very frequent or infrequent catastrophic disturbance events. Any short-term efforts designed to stimulate *C. arizonica* reproduction should be addressed to the elimination of fire suppression policies in regions of its occurrence. Long-term preservation of this locally dispersed, intolerant species requires that open habitats continue to be created by catastrophic perturbations with a frequency of recurrence greater than the age of first viable seed production, and less than the life span of the individuals in the population.

LITERATURE CITED

BANNAN, M. W. 1954. The wood structure of some Arizonan and Californian species of *Cupressus*. Can. J. Bot. 32:285-307.

BROWN, D. E., AND C. H. LOWE. 1974. A digitized computer-compatible classification for natural and potential vegetation in the Southwest with particular reference to Arizona. J. Ariz. Acad. Sci. 9. Suppl. 2, 3-11.

BRYSON, R. A., AND W. P. LOWRY. 1955. Synoptic climatology of the Arizona summer precipitation singularity. Bull. Am. Met. Soc. 36:329-339.

CATTELINO, P. J., I. R. NOBLE, R. O. SLAYTER, AND S. R. KESSELL. 1979. Predicting the multiple pathways of plant succession. Environ. Mgt. 3.41-50.

DAUBENMIRE, R. F. 1968. Plant communities. Harper and Row, New York. 300 pp.

FENNEMAN, N. M. 1931. Physiography of the western United States. McGraw-Hill Book Co., New York. 534 pp.

GLOCK, W. S., AND S. AGERTER. 1963. Anomalous patterns in tree rings. Endeavour 22:9-13.

JENNY, H., S. P. GESSEL, AND F. T. BINGHAM. 1949. Comparative study of decomposition rates of organic matter in temperate and tropical regions. Soil Sci. 68:419-432.

KEARNEY, T. H., AND R. H. PEEBLES. 1960. Arizona flora. 2d ed. University of California Press, Berkeley. 1085 pp.

NOBLE, I. R., AND R. O. SLATYER. 1977. Post-fire succession of plants in Mediterranean ecosystems. Pages 27–36 in H. A. Mooney and C. E. Conrad, tech. coords., Proceedings of the symposium on the environmental consequences of fire and fuel management in Mediterranean climate ecosystems. USDA. Forest Service Gen. Tech. Rep. WO-3. 498 pp.

PARKER, A. J. 1980. Site preferences and community characteristics of Cupressus arizonica Greene (Cupressaceae) in southeastern Arizona. Southwestern Naturalist. In press.

POSEY, C. E., AND J. F. GOGGANS. 1967. Observations on species of cypress indigenous to the United States. Auburn Univ. Agric. Expt. Sta. Circ. 153. 19 pp.

SUDWORTH, G. B. 1915. The cypress and juniper trees of the Rocky Mountain region. USDA Bull. 207:1–35.

WHITTAKER, R. H., AND W. A. NIERING. 1965. Vegetation of the Santa Catalina Mountains, Arizona: a gradient analysis of the south slope. Ecology 46:429–452.

WOLF, C. B. 1948a. Taxonomic and distributional studies of the New World cypresses. El Aliso 1:1–250.
_____. 1948b. Horticultural studies and experiments on the New World cypresses. El Aliso 1:325–444.